

Observations on Drought Resistance in *Selaginella densa* Rydb.

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INTRODUCTION.—During a recent study of *Selaginella densa* Rydb., the Prairie Club Moss, it was noted that this plant has a remarkable ability to survive conditions of extreme drought. The purpose of this paper is to record some observations made on a small mat of *S. densa* in the laboratory, and to make some remarks about drought resistance in this species. According to Maximov (1935), drought resistance can be defined as "the capacity of plants to endure drought and to recover readily after permanent wilting, with the minimum of damage to the plant itself." In the xerophytic species of *Selaginella* there is no outward appearance of permanent wilting. Probably the best evidence of reaching the permanent wilting point in these species is the tight folding of the leaves next to the stem (Daubenmire, 1959). He further stated that it is important to distinguish plants which can really endure drought (that is, plants which are drought resistant) from those which merely escape or evade drought (e.g. desert ephemerals). Drought resistance has been described for several mosses and liverworts as well as for *Selaginella*.

Campbell (1930) noted that among the California species of the Marchantiaceae, many dry up during the summer and are revived with the coming of rains in autumn. In these species, *Fimbriaria californica*, *Targionia hypophylla*, and *Cryptomitrium tenerum*, to cite a few examples, the growing point and neighboring tissues of the thallus survive. Richards (1932) described examples of drought resistance among mosses. Leaves of *Tortella inclinata* were air-dried for eighty weeks at room temperature and survived, and those of *Grimmia pulvinata* survived sixty weeks in a desiccator at 20 degrees centigrade. Stems and buds of these species were found to be even more resistant to drying. Shuster (1955) reported a case in which material of the liverwort *Riccia atromarginata* from Texas had been revived after one year and three months of drying. Growth

was evident five days after the material had been moistened, and the plants continued to grow in a greenhouse for nearly a year.

Certain species of *Selaginella* also exhibit drought resistance, the most familiar example being *S. lepidophylla*, commonly called the Resurrection Plant. Leclerc du Sablon (1889) noted the capacity of this species to withstand prolonged periods of desiccation, the plant remaining in a tight rolled-up ball in the dry state. After the application of water, it unrolls, the branches take on a green color, and growth resumes. Uphof (1920) concluded that about six per cent of the then-known 580 species of *Selaginella* are xerophytes. He discussed the anatomical features of this small group of species as well as the possible mechanism by which the cells of these plants protect their protoplasm during drought. Finally, Tryon (1955) reported that part of a mat of *S. densa* var. *densa* that had been stored for six months as an herbarium specimen grew after being planted and watered.

HABIT AND ECOLOGY.—*S. densa* is considered to be an ally of *S. rupestris*, resembling this species very closely. However, *S. densa* is usually more western in its range, occurring from southwestern Manitoba to southern Alaska, and south to Texas, Arizona, and northern California (Tryon, 1955). It grows in the form of dense mats, with short, decumbent branches. The shoot possesses a helical phyllotaxy. The branching pattern is terminal and unequal, resulting in one shank being slightly smaller than the other. Four-angled cones or strobili arise at the ends of the branches. These grow in an upright position and may reach a length exceeding one centimeter. The cones contain both microsporangia and megasporangia, the sporangial arrangement fitting Pattern I in the scheme set forth by Horner and Arnott (1963). In this pattern, there is a basal zone of megasporangia above which is a zone of microsporangia.

On the Saskatchewan prairie, *S. densa* must be considered an important part of the vegetation, covering up to twenty-five

per cent of the soil surface in some areas (Coupland, 1950). This species grows in relatively open places where it is subjected to the extremes of a severe continental climate. During much of the year the Saskatchewan prairie gets little precipitation (Table 1). During prolonged dry periods the mats are composed of dormant shoots having a dull grayish-green color and non-living shoots which exhibit an ash-gray appearance. In the dormant state the leaves, each with a long white awn on the tip, are closely appressed to the stem (fig. 1). It has been suggested by Uphof (1920) that these awns serve to reflect sunlight away from the plant as well as to protect the growing point of the stem.

In the field it was observed that the dormant aspect described above changes literally overnight if any amount of moisture becomes available to the plant. In the field after a rainfall, the grayish-green color gives way to a more luxuriant dark green, giving the previously dormant mats the appearance of active growth. On the other hand, the ash-gray color of the dead stems noted above does not change. In the active shoots, the leaves are no longer closely appressed to the stem, but lie at an angle to the axis. The appearance of a healthy and actively growing mat of *S. densa* is seen in fig. 2.

Table 1. Precipitation in Saskatoon, Saskatchewan, Canada (60 year average). Data courtesy of Physics Department, University of Saskatchewan

Inches		Inches	
Jan.	0.56	July	2.36
Feb.	0.53	Aug.	1.73
Mar.	0.59	Sept.	1.38
Apr.	0.74	Oct.	0.78
May	1.37	Nov.	0.55
June	2.54	Dec.	0.51
		Total	13.64

EXPERIMENTAL OBSERVATIONS.—In September, 1960, a sod containing a mat of *S. densa* was brought into the laboratory for observation and study. A piece of this clump that was not

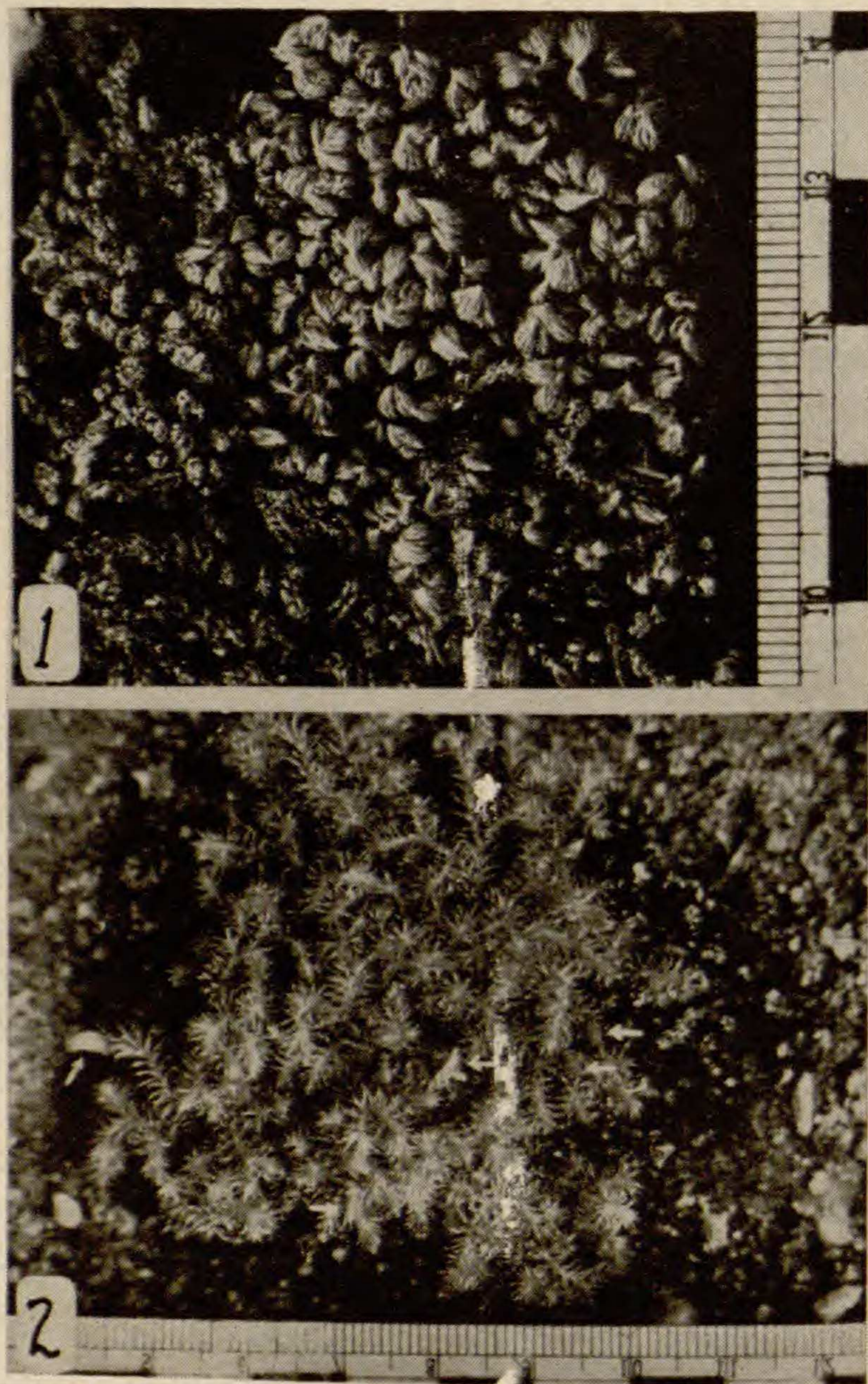


FIGURE 1. DORMANT MAT OF *S. DENSA*. SCALE IN CENTIMETERS.
 FIGURE 2. THE SAME MAT 2 MONTHS AND 27 DAYS AFTER INITIAL WATERING.
 ARROWS INDICATE CONES. SCALE IN CENTIMETERS.

used was placed on a shelf where it lay without moisture for two years. Several times during this period small pieces of the clump were removed and watered. In a few hours the dormant shoots took on the aspect exhibited by actively growing shoots. Having observed this interesting phenomenon, it was decided to test the ability of the remaining mat of dormant *S. densa* to survive a more prolonged period of dessication.

On June 17, 1963, about two years and nine months from the date of original collection in 1960, the remaining clump of *S. densa* was photographed in its dry state (fig. 1). It was then placed in a shallow dish of tap water. After two hours a change was noticeable. In some of the shoots the leaves no longer clasped the stem, but had spread and turned green, exhibiting the revived condition. The next observations were made nineteen hours after the application of water, and it could be seen that the whole mat (except the ash-gray non-living material) had the appearance of active growth. The small clump was planted in fine sand in a clay pot, placed near an eastward facing window, and watered daily. Fig. 2 shows the mat almost three months after it had first been watered. Growth is clearly evident by this time, the best evidence being the production of cones, which were absent from the original mat. At the present time several of the cones are in various states of development; some have completely shed or are currently shedding their spores, while others exhibit sporangia at different states of maturation. At certain times during this project the clump has become dry, and a return to the dormant condition has resulted. However, with the addition of water, the mat of *S. densa* has always revived quickly with no apparent damage to the plant—further verification of the drought resistance of this species.

DISCUSSION.—Tryon (1955) pointed out that, in general, the allies of *S. rupestris* are restricted in their distribution to open habitats, which are frequently xeric. He further stated that they are able to persist in such areas because of their

ability to survive desiccation. In his opinion, this ability lies in the physical and chemical properties of the contents of the cells. Such an explanation is supported by field observations on *S. densa*. In one particular site near Saskatoon, Saskatchewan, abundant sporelings at all stages of development were encountered. Over fifty locations of sporelings (or in some cases small groups of sporelings growing together) were marked with stakes, and periodic checks have been made over a period of one year and three months. It is clear from the observations made so far, that these sporelings, no matter how small (fig. 3), can survive the long periods of drought. Their fragile construction suggests that the ability to resist drought lies in some physiological mechanism of the cells themselves.

Such a mechanism has not as yet been explained for xerophytic Selaginellas, but certain information suggesting possible mechanisms should be mentioned. Leclerc du Sablon (1889) early suggested that there is a reserve substance in the cells of



FIGURE 3. SPORELINGS OF *S. DENSA*. \times 4.5.

S. lepidophylla which he thought might be responsible for the resistance of this plant to desiccation. He compared the appearance of the dense opaque protoplasm of the cells to what one sees in cells of cotyledons or in the endosperm cells of certain seeds.

In a paper dealing mainly with anatomical features of xerophytic species of *Selaginella*, Uphof (1920) concluded that the main question arising from his study is that of the protection and behavior of the protoplast of the cells under conditions of extreme drought. In cutting sections for microscopic examination, Uphof noticed many large oval-shaped droplets, which were found to be oil, coming from the open cells. During plasmolysis of the cell, the oil droplets fuse to produce larger ones. Uphof suggested that when the cells lose water, a film of oil is formed around the vital parts of the cell, preparing the cells for dormancy during periods of drought. He noted that neither mesophytic species (e.g. *S. galeottii*) nor xerophytic *Selaginellas* grown under conditions of abundant moisture produce oil. Evans (1958, 1959) found that in certain filamentous algae which are able to survive drought, the vegetative cells become modified with accumulations of oil. Other changes that he noted for these cells are thickened walls and mucilaginous sheaths.

In a recent work by Iljin (1957), possible mechanisms by which cells in general resist desiccation were noted. Iljin reported that, according to numerous workers, species of plants living in dry habitats have smaller cells than plants of moist habitats. Mosses, lichens, algae and other lower plants adapted to dry locations were cited as having cells of small volume. Uphof (1920) noted this feature for the xylem elements and cortical cells of xerophytic species of *Selaginella*. Iljin suggested that smaller cells suffer less damage under conditions of desiccation. When a cell loses water from the vacuole, the opposite walls are caused to approach one another so that the desiccated cells may become separated. In larger cells, there

would be a greater readjustment of the walls to each other and more possibility of damage than in smaller cells.

The authors wish to express their appreciation to Dr. M. V. S. Raju and Mr. Norman Ferrier for aid in photography. They also wish to express their indebtedness to Mr. Ted Cooper for assistance in laboratory and field work and to Dr. William C. Steere for his helpful suggestions. This investigation was supported by a grant from the National Research Council of Canada.

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